THE VEGETATION ON COASTAL DOGTOOTH LIMESTONE IN SOUTHERN CUBA

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With One Plate

ONE OF THE GEOLOGIC FEATURES of the southern coast of Las Villas province in Central Cuba is an uplifted bench of weathered limestone known in Cuba as diente de perro or dogtooth limestone. The name describes well the lacerated, sharp-edged, hard, metallic-ringing limestone rock (PL. I, FIG. 1). Similar formations exist in a few other spots in Cuba, on the islands off Haiti and the Dominican Republic, and near Ponce in Puerto Rico; but they appear to be found principally on the southern coasts. They are missing in the Lesser Antilles and Jamaica, and are not comparable to the limestone formations of the Bahamas. The formation is covered with a tree and shrub vegetation which has never been described adequately. Gleason and Cook (Scientific Survey of Puerto Rico and the Virgin Islands 7: 158. 1927) describe briefly a "xerophytic forest" on the Ponce limestone. Ekman (Ark. för Botanik **22A**(16) : 4. 1929) lists the components of this vegetation as found on Navassa Island. The senior author has considerable unpublished data for the vegetation of Beata Island, off Hispaniola, which is also growing on dogtooth limestone. These four areas seem comparable in aspect of the vegetation and substratum, but the floristic composition of the vegetation is different in each case. The present paper records the elements comprising the predominantly woody vegetation on the dogtooth limestone in Cuba.

Coastal exposures of dogtooth limestone are found in Las Villas province on either side of the entrance to Cienfuegos Bay. The exposures, paralleling the coast, extend east from Punta Caballos to the mouth of the San Juan river, and west from Castillo de Jagua to the edge of the Cienaga de Zapata. The flora in this area has been collected by several botanists in the past few decades. John George Jack of the Arnold Arboretum collected intensively during the late 1920's in the region discussed in this paper, but he failed to leave any significant notes on the composition of the woodland formation. Combs (Trans. Acad. Sci. St. Louis, 7: 393–491. 1897) studied the area west of Cienfuegos Bay, primarily around Castillo de Jagua, but he too failed to describe the vegetation. Ekman apparently never visited the area during his work in Cuba, and Leon and his associates have not described it.

The area selected for study is a portion of the Gavilan tract owned by the

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Central Soledad. It is west of the Rio Gavilan and east of Punta Lobos and the mouth of Cienfuegos Bay. The specific area is known locally as the Potrero Seboruco and is adjacent to the small Playa de Gavilan.

The south coast of Las Villas province in this area has an undulating shoreline. In a very few of the embayments are sandy beaches. The major portion of the shoreline consists of limestone benches slightly below, at, or slightly (1–3 feet) above sea level. The benches represent a relatively small vertical land adjustment of recent origin. When exposed they are covered with a low shrub growth, littoral in nature, consisting of *Rachicallis americana, Strumpfia maritima,* and *Conocarpus erectus.* Directly behind this coastal formation is a sharply uplifted block of limestone of Miocene age. It is the vegetation of this block that is considered in the present paper. The average uplift appears to be between 15 and 25 feet. The southern edge of the block is wave cut, with a series of erosion caverns indicating that the area, within relatively recent time, was at the sea margin. The uplifted limestone block dips slightly to the north, and ends in an open lateritic plain of reddish soil with a savannah type of vegetation.

The limestone block parallels the coast, and the region studied is approximately one-half mile wide. The formation has been cracked by subsequent land movements. Some of the larger sections are flat-topped, perfectly smooth and show little sign of weathering except at the fractures. At the coastal margins, however, sections of the block are severely cracked and show both large and small chasms, narrow and wide, extending down to sea level. One chasm (PL. I, FIG. 2) is 150 feet long and 25 feet deep and averages 25 feet in width. In this chasm a shallow lake of brackish water has developed. The bottom of the shallow lake is of soft debris and muck, and it was impossible to walk in it.

The smaller sections of the main block, especially those at the southern edge, are severely weathered with each section rounded to the middle (PL. I, FIG. 1). The rock is extremely hard and the results of weathering have been peculiar. A matrix of extremely sharp and hard ridges and spines has been developed (PL. I, FIG. 1). According to Lewis (Amer. Assn. Petr. Geol. Bull. **16**: 533–555. 1932) this weathering is not due to the erosion of a softer rock from a harder matrix, as the rock is essentially homogeneous, but rather due to extremes of temperature, humidity, and rainfall, external physical conditions. Loose fragments of the rock will ring with a characteristic metallic sound when struck. Footing is treacherous on these naked sharp ridges, and the name "dogtooth limestone" for such an area is well deserved. Similar lacerated surfaces are found only on the edges of the larger fracture blocks.

The entire surface in this area can be described as naked rock. The mass is so cracked and weathered into a porous structure that only rarely have very small, cup sized pockets of soil accumulated. The leaves and branches present on the surface are dry and no humus has been formed. However inhospitable the area seems, the limestone block is covered with a shrub and tree vegetation. In most areas this vegetation is open. The trees average 35 feet in height and are unbranched for the first 15 feet. The

boles are thick and massive for the heights of the trees, and are generally crooked. The crowns are symmetrical and the effects of the wind have not caused the lopsided growth expected in coastal vegetation. The shrub vegetation is approximately 12 feet in height, usually densely branched and predominantly spiny. Herbaceous vegetation is almost entirely lacking and no ferns were seen. Shade loving plants are conspicuously absent under the thin and open canopy. Epiphytes are relatively abundant but only members of the Bromeliaceae were found. Vines are few but the individual plants are usually extensive.

Root development of all plants found on the dogtooth limestone is conspicuous, perhaps because one is not accustomed to seeing the roots of tropical trees. Unless the plants are growing in or near a rock chasm the roots usually crawled along the surface to a distance greater than the radius of the crown before penetrating into cracks in the rocky substratum. The trees seem to be successful in such an area because the roots are able to penetrate to a depth where moisture is available.

In order to determine accurately the composition of this vegetation we ran a transect through the vegetation on the limestone outcrop. The senior author [1] had surveyed the region several years before in order to determine the most undisturbed locality and to learn the nature of the flora. Several survey trips were made before and after the date of the transect to ascertain the extent to which the transect was typical. It was determined that the area studied was characteristic of the vegetation occurring on the limestone, and that relatively few more species were to be expected than were seen on the transect.

The transect made was 880 yards long and 2 yards wide. Every plant within this strip, the area of which is $\frac{1}{3}$ acre, was counted. Stem diameters of all woody species were determined at breast height.

The vegetation of the transect area consists of 74 species and 521 individual plants, excluding only the epiphytes and parasites. The detailed composition is shown in the following table:

Trees:	22 species	29.7%	of total	—	231 individuals	44.3%	of total
Shrubs:	35 species	47.2%	of total	—	224 individuals	42.9%	of total
Herbs:	9 species	12.1%	of total	—	30 individuals	5.7%	of total
Vines:	8 species	10.8%	of total	—	36 individuals	6.9%	of total
Total:	74 species	99.8%			521 individuals	99.8%	

While shrubs dominate the area from the standpoint of the number of species involved, the trees are slightly more significant from the standpoint of number of plants. The herbaceous species, vines, and epiphytes make up a relatively unimportant aspect of the vegetation on the dogtooth limestone.

[1] The authors are grateful for the assistance of the other members of the course in Tropical Botany of Harvard University who helped on this survey. Special appreciation is acknowledged for the suggestions and help of Mr. Earl E. Smith in the recording method used. They also wish to thank the management of Central Soledad for permission to study the area.

SPECIES	LESS THAN 3″	3″	4″	5″	6″	7″	8″	9″	10″	12″	15″	16″	TOTAL
Gymnanthes lucida	31	18	9	2									60
Cordia Gerascanthus	32	7		1									40
Leucaena glauca	26	1	3	1	1								32
Hebestigma cubensis	10	1	4	1	4	1	2	1		2			26
Celtis trinervia	6			3	1								10
Pseudocarpidium Wrightii	5		2					1	1				9
Adelia ricinella	7		1										8
Tabebuia pterophila	5	1		1									7
Torrubia discolor	1	2	1							1	1	1	7
Exostema caribaeum	3				1	1							5
Capparis cynaphallophora	4		1										5
Colubrina reclinata	3		1		1								5
Vitex divaricata	1		1			1							3
Bursera simaruba	1								1				2
Luhea speciosa						1							1
Hypelate trifoliata									1				1
Securinega Acidoton				1									1
Rondeletia pedicellaris		1											1

THE SIGNIFICANT COMPONENTS OF THE VEGETATION ON DOGTOOTH LIMESTONE IN CUBA LISTED BY DIAMETERS OF THE BOLES AND FREQUENCY OF OCCURRENCE.

The trees were tabulated for their frequency and size. All trees with a trunk diameter of less than three inches were considered together. Any plant with an unbranched bole of ten feet was considered to be a tree possessing a potentially useful log. *Casearia sylvestris*, represented by three specimens, and *Forestiera laevigatus* by one specimen, have the necessary length of trunk but none of the specimens exceed three inches in diameter at breast height. One large specimen of *Ficus laevigatus* defied classification in possessing multiple trunks, several of which were eight inches in diameter. A lone specimen of *Ceiba pentandra* towers over the rest of the trees on this limestone and has a trunk diameter of 36 inches; however, the wood of the *Ceiba* is considered worthless. The remaining 18 arboreal species are listed in the following table, in order of their frequency of occurrence. All size figures represent diameters at breast height.

It can be seen from the table that *Hebestigma cubensis* and *Torrubia discolor* are the only potential timber trees in the transect. *Gymnanthes lucida*, *Cordia Gerascanthus*, and *Leucaena glauca* appear to be the only trees seeding themselves, as indicated in the number of saplings encountered. None of the species in the above list is currently considered valuable as a timber tree.

The shrubs of the transect have trunks less than six feet long to the first branch, or are characteristically bushy in appearance. They comprise the following species. The number of individuals counted in the transect follows each species.

Erythroxylum areolatum	72	*Lantana reticulata*	4
Argythamnia candicans	28	*Leucocroton microphylla*	3
Pithecellobium Hysterix	15	*Capparis flexuosa*	3
Cordia globosa	14	*Schaefferia frutescens*	3
Croton lucidus	14	*Malpighia cubensis*	3
Hyperbaena racemosa	13	*Guettarda elliptica*	3
Acacia farnesiana	10	*Erythroxylum rotundifolium*	3
Duranta repens	7	*Plumiera obtusa*	3
Capparis Grisebachii	5	*Randia spinifex*	2
Boerreria succulenta	4		

Single specimens of the following species were found: *Citharexylum spinosum*, *Amyris elemifera*, *Boerreria virgata*, *Caesalpinia glaucophylla*, *Phyllanthus neopeltandrus*, *Guettarda Combsii*, *Bumelia glomerata*, *Guaiacum sanctum*, *Savia sessiliflora*, *Comocladia dentata*, *Guettarda calyptrata*, *Anthacanthus tetrastichus*, *Pluchea odorata*, *Rhacoma Crossopetalum*, *Celtis iguanaea*, and *Morinda Royoc*.

Erythroxylum areolatum dominates the shrubs in the transect area. The plants of this species average eight feet in height and fruit heavily. They usually occur in groups. It is probable that birds are responsible for the dispersal of the red-colored fruits. *Argythamnia candicans*, generally a 3–4′ woody shrub, is represented by hundreds of seedlings. The fruits of this member of the Euphorbiaceae are elastically dehiscent. *Argythamnia*

is the only plant that appears to be spreading rapidly. *Comocladia dentata* is more abundant outside of the transect area, particularly in the inland lateritic soil zone. *Celtis iguanaea* is represented by one shrub, rooted far down in one of the larger chasms and climbing on the limestone rocks before scrambling into the tree tops. Some of the branches of this plant are 2″ in diameter and reach a length of 25 feet.

The herbaceous plants and cacti are represented by nine species. *Hibiscus pilosus* is most abundant with individuals counted. *Setaria distantiflorum*, represented by three individuals in the transect area, is growing on very small pockets of soil in the dogtooth limestone. *Ayenia pulsilla*, *Acalypha chamaedrifolia* and *Portulaca pilosa* are all on the limestone, but only single individuals were seen. Sterile plants of *Harrisia*, *Selenicereus*, and *Cephalocereus* were found. *Opuntia Dillenii* is represented by one flowering and fruiting plant which forms an extensive sprawling mass.

Of the eight species of vines in the transect area *Stigmaphyllon Sagraeanum* is the most abundant with fifteen individuals counted. *Serjania subdentata* was found nine times, and *Triopteris rigida* and *Passiflora suberosa* four times for each. Two extensive plants of *Acacia tenuifolia*, a viciously spiny species were found, and single specimens of *Urechites lutea*, *Gouania polygama* and *Tournefortia peruviana*.

One parasite, *Phthirusa purpurea* was found growing on *Tabebuia pterophila*. Three species of *Tillandsia* were the only epiphytes seen. These plants are numerous and were not considered in the transect count. *Tillandsia fasciculata* is the most abundant, while *T. flexuosa* and *T. tenuifolia* are infrequent.

In an area such as the dogtooth limestone, where soil cover is lacking, moisture penetration is high, the canopy thin, and the temperature high, evaporation and transpiration are assumed to be critical factors in the environment. Various morphological specializations are expected in plants capable of living in such an environment. These specializations are generally expressed in reduced total leaf surface, microphyllous leaves which are usually associated with the presence of spines, thick cuticles, and ilicioid leaves. If the leaves are large, they usually have soft laminal tissues and are apt to wilt and droop easily. Of the species found in this area, five of the trees, five of the shrubs, and one of the vines possess microphylls. Such leaves are generally of hard thick tissues. Spines, either modified branches or of stipular origin, are found in one of the trees, seven of the shrubs and one of the vines. Ilicioid leaves occur in one species of the trees and one of the shrubs. The wilting habit was especially obvious. On the hot sunny day when the transect was made nearly 50% of the broad leafed species appeared to be in a wilting condition.

Exact rainfall data for this specific area are not available. The site is to the west of the normal path of rain storms from the Trinidad-San Juan mountains. The rainfall is probably in the range of 30–35 inches, which is commonly regarded as insufficient, in the Caribbean area, to support other than a thorn-shrub type of woodland. The lack of surface accumula-

tion of soil and moisture may account for the lack of herbaceous plants and the deep penetration of the roots of the shrubs and trees.

It is probable that the woody vegetation found on the dogtooth limestone is a fairly stable type for this habitat under existing environmental conditions. While the sea side cliff development indicates former proximity to the Caribbean Sea there is, at present, no indication of the littoral or halophyte shrub vegetation characteristic of the low limestone coastal formations in Cuba.

The current vegetation of the area meets the description of a thorn woodland proposed by Beard (Ecology **25**: 140. 1944) but does not fit into any of the fascies he suggested. In general aspect it agrees with the descriptions published by Ekman for the dogtooth limestone areas of Navassa Island, and by Gleason and Cook for the Ponce limestone. In floristic composition and species dominance, however, it is quite different. Ekman described the forests of the dogtooth limestone of Navassa Island as "low, the trees are stunted, though often with thick trunks. Characteristic of Navassa is the small number of species involved. Only four species of trees could be labelled as common, to wit, *Ficus populnea*, *Sideroxylon foetidissimum*, *Coccoloba laurifolia*, and *Metopium Brownei*. Scatter occur: *Pseudophoenix navassana*, *Bumelia navassana*, while *Fagara martinicensis* and *Colubrina feruginosa* are rare. Shrubs are few, e.g. *Pisonia discolor* var., *Schoepfia obovata*, and *Duranta erecta*, while vines and epiphytes are nearly absent." (Ark. för Botanik, **22A** (16): 4. 1929).

Gleason and Cook (Sci. Surv. Puerto Rico and Virgin Is. 7: 158. 1927) report the composition of the "xerophytic forest" on the Ponce limestone as follows: "Trees, *Bursera simaruba*, the commonest trees, *Bucida buceras*, *Ficus laevigatus*, *Amyris elemifera*, *Capparis cynophallophora*, and *Pisonia albida*. Rare or scattered trees of *Guaiacum officinale* and *Tabebuia heterophylla*. The shrub layer comprises a large number of species of which *Lantana involucrata*, *Coccolobis laurifolia*, *Helicteres jamaicensis* seem to be the most abundant. Other common species are *Moluchia tomentosa*, *Croton rigidus*, *Croton lucidus*, *Exostema caribaeum*, *Varronia angustifolia*, *Savia sessiliflora*, *Pithecellobium Unguis-cati*, *Ricinella Ricinella*, *Eugenia ligustrina*, *Eugenia buxifolia*, *Schaefferia frutescens*, *Hypelate trifoliata*, *Reynosia uncinata*, *Samyda dodecandra*, *Citharexylum fruticosum*, *Plumeria alba*, *Adelia Bernardia*, *Krugiodendron ferreum*, *Elaeodendrum xylocarpum*, *Comocladia Dodonea*, *Canella Winteriana*, *Jacquinia Berterii* and *Tournefortia microphylla*."

A comparison of the list of plants found on the Las Villas dogtooth limestone to those listed above by Ekman and by Gleason and Cook emphasizes the similarity of aspect among the dogtooth limestone floras as well as the differences in species and dominants comprising them.

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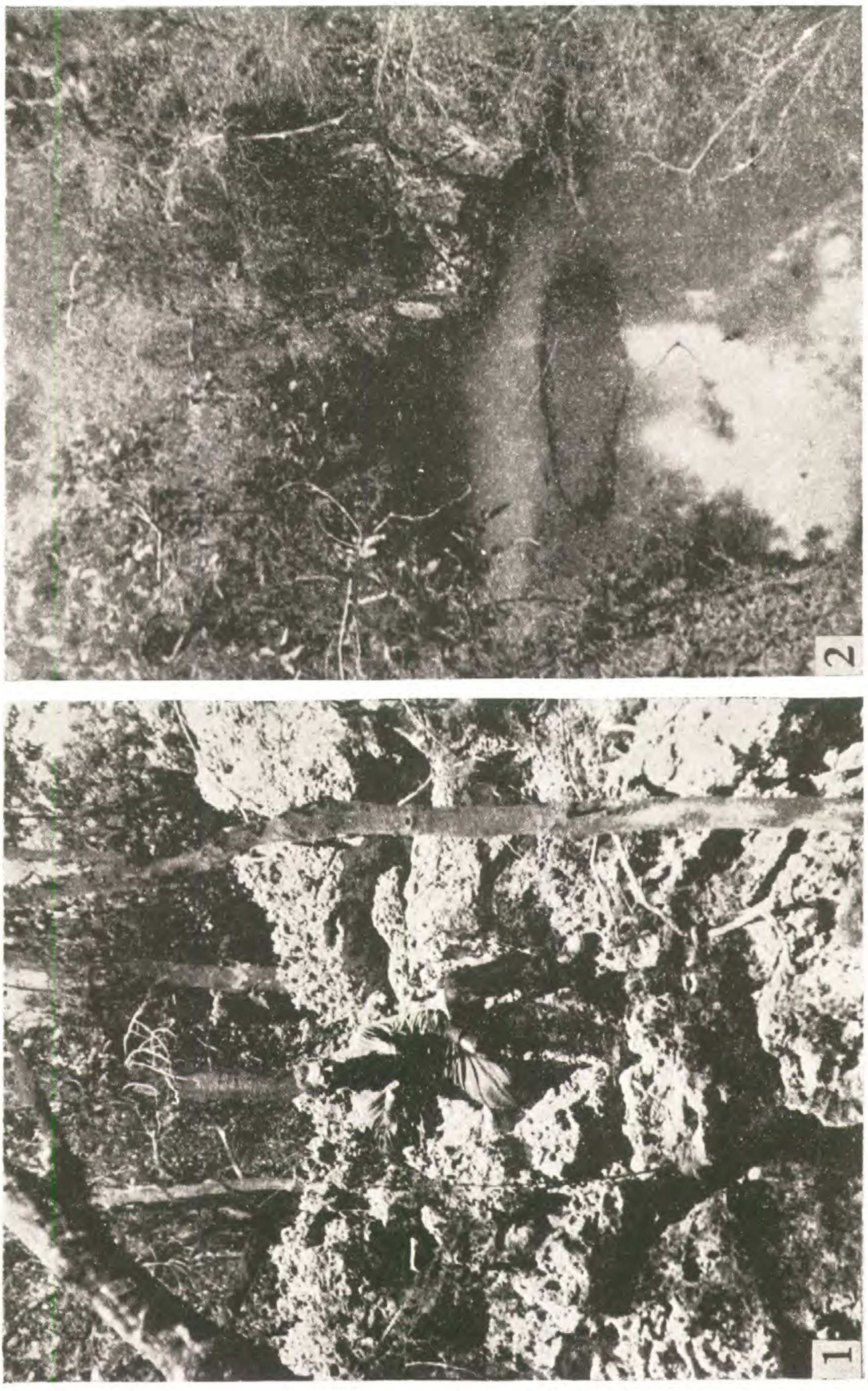
EXPLANATION OF PLATE

FIG. 1. The face of one of the smaller chasms in the Gavilan dogtooth limestone showing the many cracks and the eroded surface with sharp projections.

FIG. 2. A larger chasm in the limestone block showing a shallow brackish lake.



HOWARD & BRIGGS, VEGETATION ON DOGTOOTH LIMESTONE